

Host Plant Choice Experiments of Colorado Potato Beetle (Coleoptera: Chrysomelidae) in Virginia

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ABSTRACT Field and laboratory-choice experiments were conducted to understand aspects of host plant orientation by the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae), in Virginia. In laboratory bioassays, *L. decemlineata* oriented to volatiles emitted by potato, *Solanum tuberosum* L., foliage over both tomato, *Lycopersicon esculentum* L., and eggplant, *Solanum melongena* L., foliage, and eggplant over tomato foliage, all of which had been mechanically damaged. Field choice tests revealed more *L. decemlineata* adults, larvae, and egg masses on eggplant than on tomato. In other experiments, counts of live *L. decemlineata* on untreated paired plants and counts of dead beetles on imidacloprid-treated plants did not differ between potato and eggplant. *L. decemlineata* was significantly attracted to eggplant over both tomato and pepper. To determine whether feeding adults affected orientation to host plants, an imidacloprid-treated eggplant or potato plant was paired with an untreated eggplant or potato plant covered in a mesh bag containing two adult male beetles. Significantly more adults were attracted to eggplant with feeding male beetles paired with another eggplant than any other treatment combination. These results indicate that the presence of male *L. decemlineata* on plants affects host plant orientation and suggests that the male-produced aggregation pheromone may be involved.

KEY WORDS eggplant, solanaceous, *Leptinotarsa decemlineata*, potato, tomato

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), is considered one of the most destructive pests of potato, *Solanum tuberosum* L., in North America, Europe and Asia. It also feeds on other solanaceous plants, including eggplant, *Solanum melongena* L., and tomato, *Lycopersicon esculentum* L. (Hare 1990, Jacques 2005).

Understanding host plant selection of *L. decemlineata* may provide information for the development of alternative control strategies, such as trap cropping (Hunt and Whitfield 1996) or host plant resistance. *L. decemlineata* probably originated in South America, where it fed primarily on the wild host buffalo burr, *Solanum rostratum* Dunal (Walsh 1865). Although *L. decemlineata* feeds on a variety of native and exotic solanaceous plants (Brues 1940, Hsiao and Fraenkel 1968, Jacques 1988, Hare 1990), feeding and oviposi-

tion choices for one solanaceous species over another have been noted. Based on field observations, Walsh (1865) suspected that *L. decemlineata* preferred eggplant over potato and potato over tomato based on the botanical similarity of these host plants to the wild host buffalo burr. In Massachusetts, *L. decemlineata* were noted on buffalo burr, eggplant, and potato, but they were unable to survive for more than two seasons on other potential host plants (*Solanum subinerme* Jacquin., *Solanum marginatum* L., *Solanum dulcamara* L., *Solanum torvum* Swartz, *Solanum barbisetum* Nees, and tomato) (Brues 1940). Several researchers have identified potato as a preferred host for *L. decemlineata* (Hsiao and Fraenkel 1968, De Wilde and Hsiao 1981, Matsuda 1988, Hare 1990); however, other solanaceous crops such as eggplant, tomato, and pepper, *Capsicum annum* L., as well as solanaceous weeds such as nightshades and nettles have been noted as suitable hosts (Hsiao and Fraenkel 1968, Hare 1990). To better understand host plant choice of native *L. decemlineata* in Virginia and factors that may contribute to these choices, we conducted field- and laboratory-choice experiments by using solanaceous crops available to local *L. decemlineata* populations in the field in Virginia. We also sought to determine whether the presence of colonizing male *L. decemlineata* adults feeding on eggplant or potato affected the number of new *L. decemlineata* adults coming to those plants in the field.

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Materials and Methods

All laboratory and field experiments were conducted at the Virginia Tech Eastern Shore Agricultural Research and Extension Center (ESAREC) in Painter, VA. For all experiments, we used 'Superior' potato, 'Black Beauty' eggplant, 'Florida 47' tomato, and 'Paladin' bell pepper. Although Paladin bell pepper was initially included in one of our field experiments, it was not used in other experiments after we observed no *L. decemlineata* on plants in the field and no feeding or beetle development on caged plants (unpublished data).

Olfactory Laboratory Comparison. *L. decemlineata* adults, collected within 1–2 d of emergence from the soil in May, were used for olfactometer studies. Beetles were collected from untreated potato plants in the field, and they were taken to the laboratory where they were sexed using the distinctive projections on the last ventral abdominal segment (Rivnay 1928). Beetles were placed individually in petri dishes with a moistened cotton ball.

An open Y-track olfactometer ("Flying T") apparatus modified after Visser and Piron (1998) and described in detail by Dickens (1999) was used for laboratory choice experiments. Hydrocarbon-free air, supplied at the rate of 1 liter/min, was humidified by passing it through distilled water before delivery of the plant volatiles to the apparatus. Beetles were considered to have made a choice after traveling 1 cm up either arm of the Flying T. Foliage was replenished after 30 min.

Experiments were conducted in a darkened room (24°C) in which the only light source was from the bioassay apparatus. For each assay, 20 adult males and 20 adult females were tested. Beetles were starved for 24 h then dark adapted for 1 h before testing. The following tests were conducted: potato versus tomato, potato versus eggplant, and eggplant versus tomato. Eggplant foliage and tomato foliage were obtained from 10- to 12-wk-old plants potted in Pro-mix potting soil/vermiculite mix (\approx 4-liter pots), whereas potato foliage was obtained from field-grown potato plants. Plants ranged in height from 25 to 35 cm. For each of the three plant species tested, single-stems weighing \approx 4.8 g, were removed from the plants and mechanically injured by making \approx 1-cm slits around the perimeter of the leaf (Dickens 1999). This experiment was conducted three times, once in 2006 and twice in 2007. Each experimental bout served as a replication. Data were analyzed by testing the hypothesis that the binomial proportion was significantly different from a probability of 50% by using the standard normal approximation (Ott and Longnecker 2001).

Field Comparison Test 1: Tomato versus Eggplant versus Pepper. Field comparisons were conducted during summer 2005. Plants were seeded in the greenhouse, and then they were transplanted into the field on 19 May 2005. The three crops were transplanted into a single row so that there was a 6-m section of eggplant, a 6-m section of tomato, and a 6-m section of pepper, for a total row length of 18 m. The order of the

three crops was randomized for each replicate. There were three treatments replicated four times and arranged in a randomized complete block design: 1) all plants were treated before transplanting with a drench of imidacloprid (255.5 g [AI]/ha), 2) eggplants only were treated with the imidacloprid drench before transplanting; and 3) all plants were untreated. Preliminary observations indicated that eggplant may be more attractive than tomato or pepper; therefore, eggplant only was treated to determine whether imidacloprid treated eggplant would reduce beetle numbers in tomato or pepper. Numbers of *L. decemlineata* dead adults within 30 cm of the row, live adults, larvae, and egg masses on each crop in each block were counted twice a week for \approx 1 mo (total of seven sampling events). To meet normality assumptions, all data were transformed using a square root ($x + 0.05$) transformation before analysis. Data were subjected to one-way analysis of variance (ANOVA) at $P < 0.05$ level of significance. When significant F values were detected by ANOVA, means were separated using Fisher protected least significant difference (LSD) test (Analytical Software 1998). Untransformed data were used in all figures.

Field Comparison Test 2: Potato versus Eggplant. Field comparisons were conducted during summers 2006 and 2007 to determine whether *L. decemlineata* infestations differed between untreated potato and eggplant and insecticide-treated potato and eggplant. In 2006, the field comparisons were conducted once, whereas in 2007 the field comparisons were conducted twice by using two separate areas of the research farm (hereafter, referred to as 2007a and 2007b in tables and figures). Potatoes were planted directly in the field in March 2006 and 2007 following standard cultivation and production practices for Virginia (Kuhar et al. 2006b). Eggplants were grown in a greenhouse (Hampton Roads Agricultural Research and Extension Center, Virginia Beach, VA) and transplanted into 15-cm pots before placement in the field. The potted eggplants were buried in the soil at the start of the study so the rims of the pots were even with the soil surface. Individual plots consisted of two 1.5-m-long rows separated by 0.91 m. One row contained five potted eggplant plants, whereas the other row contained five potato plants. In the first experiment, we counted the number of live *L. decemlineata* adults on paired rows of untreated potato and eggplant. In the second experiment, we counted the number of dead *L. decemlineata* adults found on or at the base of plants in paired rows of potato and eggplant treated with imidacloprid (255.5 g [AI]/ha). Both treatments were replicated four times in each experiment.

In 2006, potato plants were carefully pruned 24 h before the start of the study to approximately match the visually estimated leaf area in the eggplants. Plants were pruned by removing one to two stems from each potato plant with scissors. We understand that injury to potato plants as a result of pruning might change the volatile profile emitted by the plant; however, potato leaflets damaged by mechanically removing a 2-mm strip of tissue with scissors were found to be attractive

to *L. decemlineata* for only 15 min (Bolter et al. 1997). Because pruning was done 24 h before testing, and observations were made over a period of 2 wk, any prolonged effects on the attractiveness of the plants due to pruning are likely to have been minimal.

In 2006, *L. decemlineata* numbers (including dead adults and live adults) in each block were counted every 2–3 d for ≈ 2 wk (total of four sampling events). Both beetles and egg masses were removed from the plants at the end of every sampling event to avoid recounting.

Eggplants used for the 2007 study matched the leaf area of the potato plants, and they were therefore not pruned. Because *L. decemlineata* populations were low in 2007, beetles collected from nearby potato fields were released around each block on 13 and 20 June. For each release, 40 beetles were placed around the perimeter of each block (10 beetles to each side of the block). *L. decemlineata* numbers (including dead adults and live adults) in each block were counted every 2–3 d for ≈ 2 wk (total of four sampling events). For each sample date, beetles and egg masses were removed from the plants to avoid recounting.

For all field comparisons, beetle numbers were compared using a paired *t*-test at the $P < 0.05$ significance level. All data were transformed using a square root ($x + 0.05$) transformation before analysis. Untransformed data are presented in figures.

Effect of Colonizing Male *L. decemlineata* Adults Feeding on Eggplant and Potato. Experiments were initiated on 28 April 2006 and 7 May 2007 immediately after *L. decemlineata* emerged from overwintering. Six treatments were arranged in a randomized complete block design with six replicates. Replicates were separated from one another by placing them within alleyways of six-row blocks of potatoes. There were 3.7 m of bare ground and a six-row block of potatoes separating the replicates, whereas individual test plants within a replicate were separated by 9.1 m from one another.

Test plants were either eggplant or potato treated with imidacloprid drench (imidacloprid 255.5 g [AI]/ha), and they were ≈ 25 –30 cm in height at initiation of the experiment. Test plants were either paired with an imidacloprid-treated eggplant or potato plant that was covered by a mesh bag that contained two *L. decemlineata* males that had been collected from untreated potatoes. Potatoes were planted directly in the field in March 2006 and 2007, whereas eggplants were grown in a greenhouse (Hampton Roads Agricultural Research and Extension Center, Virginia Beach, VA) in 5-cm pots and obtained at the six-leaf stage in April and May for use in the experiment. Potted eggplants were placed in the soil so the rims of the pots were even with the soil surface. There were six treatments, which consisted of the following pairs of plants: 1) potato (treated) + potato (*L. decemlineata*); 2) potato (treated) + eggplant (*L. decemlineata*); 3) potato (treated) + potato (no *L. decemlineata*); 4) eggplant (treated) + potato (*L. decemlineata*); 5) eggplant (treated) + eggplant (*L. decemlineata*), and eggplant (treated) + eggplant (no *L. decemlineata*). Numbers of live and dead *L. decemlineata*

Table 1. Behavioral response of *L. decemlineata* adults to volatiles emitted by mechanically damaged foliage from solanaceous plants in a laboratory olfactometer for three combined experiments, 2006–2007

Orientation of <i>L. decemlineata</i>	Mechanically damaged plants		
	A. Potato vs. B. tomato	A. Potato vs. B. eggplant	A. Eggplant vs. B. tomato
Combined experiments 2006 and 2007	76:44	80:40	76:44
% response to A	63.3*	66.7*	63.3*

* Responses differed for paired treatments ($P < 0.01$) by testing the hypothesis that the binomial proportion is significantly different from $P = 50\%$ by using the standard normal approximation (Ott and Longnecker 2001).

adults on or within a 30-cm radius of each test plant were recorded at 24, 48, 72, and 96 h. For each evaluation, all beetles found on a test plant were removed to avoid recounting for the following evaluation. Data were analyzed by ANOVA at $P < 0.05$ level of significance. When significant *F* values were detected by ANOVA, means were separated using Fisher protected LSD test (Analytical Software 1998).

Results

Olfactometer Laboratory Comparison. Results were similar for all three experimental bouts conducted in 2006 and 2007. Significantly more *L. decemlineata* adults oriented to the odorous blend emitted from mechanically damaged foliage of potato compared with eggplant ($P < 0.01$) or tomato ($P < 0.01$) (Table 1). In addition, volatiles arising from mechanically damaged eggplant foliage were preferred by *L. decemlineata* over volatiles from mechanically damaged tomato foliage ($P < 0.01$).

Field Comparison Test 1: Tomato versus Eggplant versus Pepper. Bell pepper plants tested in the study had no *L. decemlineata* adults, larvae, or egg masses for all sample dates; therefore, they were omitted from analysis. On untreated plots (no insecticides), more *L. decemlineata* adults ($F = 18.5$; $df = 1, 82$; $P < 0.0001$), larvae ($F = 11.6$; $df = 1, 82$; $P = 0.0010$), and egg masses ($F = 10.6$; $df = 1, 82$; $P = 0.0016$) were noted on eggplants than on tomatoes (Fig. 1). In imidacloprid-treated plots, more dead *L. decemlineata* adults ($F = 8.55$; $df = 1, 82$; $P = 0.0045$) were found in eggplant plots than tomato plots (Fig. 2). Across all sampling dates, there were 297 dead *L. decemlineata* adults found in eggplant plots compared with 20 dead adults found in tomato plots. Treating eggplants only with imidacloprid in intercropping rows did not reduce the number of *L. decemlineata* adults ($F = 0.25$; $df = 1, 54$; $P = 0.6167$), larvae ($F = 0.12$; $df = 1, 54$; $P = 0.7290$), or egg masses ($F = 0.16$; $df = 1, 54$; $P = 0.6950$) on tomatoes.

Field Comparison Test 2: Potato versus Eggplant. On untreated plants across three experiments, the mean number of live *L. decemlineata* adults on eggplant and potato were generally similar (Fig. 3). In

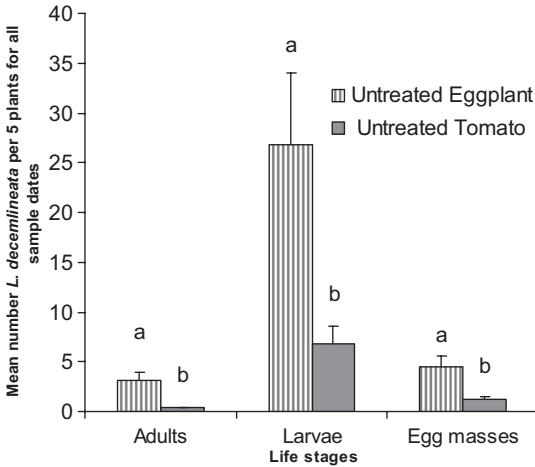


Fig. 1. Number of live *L. decemlineata* adults, larvae, and egg masses (mean \pm SE per five plants) on untreated eggplant and tomato across seven sample dates in 2005. Bars surmounted by different letters are significantly different as determined by one-way ANOVA ($P < 0.05$) and Fisher protected LSD.

2006, on only one sample date, more live *L. decemlineata* adults were found on untreated eggplant than on untreated potato ($t = 5.09$, $df = 3$, $P = 0.0147$) (Table 2).

Similarly, for the imidacloprid-treated plants, there were no significant differences in the numbers of dead *L. decemlineata* adults found on treated eggplant and treated potato in 2006 and 2007 for all sample dates (Table 2; Fig. 4).

Effect of Colonizing Male *L. decemlineata* Adults Feeding on Eggplant and Potato. There was a significant difference in the total number of *L. decemlineata* adults found coming to the test plants over time in 2006 ($F = 2.76$; $df = 5, 25$; $P = 0.0406$) and 2007 ($F = 3.12$; $df = 5, 25$; $P = 0.0252$), with the eggplant (treated) +

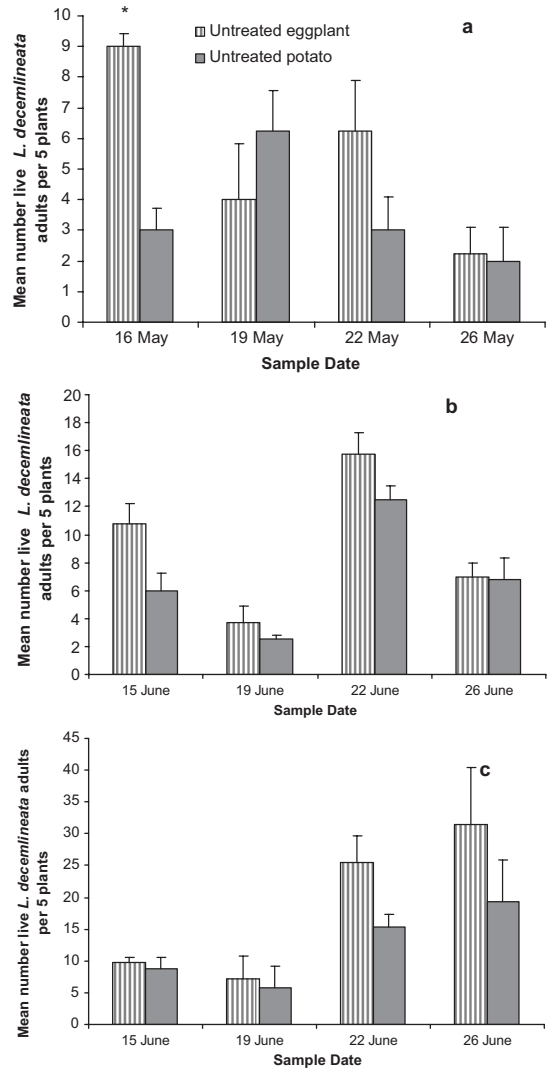


Fig. 3. Number of live *L. decemlineata* adults (mean \pm SE per five plants) found on untreated eggplant and potato paired plots for four sample dates in 2006 (a), 2007a (b), and 2007b (c). Symbols indicate significant differences at $P < 0.05$.

eggplant (*L. decemlineata*) treatment having significantly more beetles than all other treatments (Fig. 5a and b).

Discussion

Insect host plant choice is a complex phenomenon that is typically governed by a variety of factors. Both visual and olfactory cues play a key role in the location of potential host plants by *L. decemlineata* (Schanz, 1953, De Wilde et al. 1969, Visser 1976, Zehnder and Speese 1987). The use of an olfactometer in laboratory choice experiments eliminates visual plant finding variables, and it allows insight into the role that plant volatiles play in host finding or selection (McIndoo

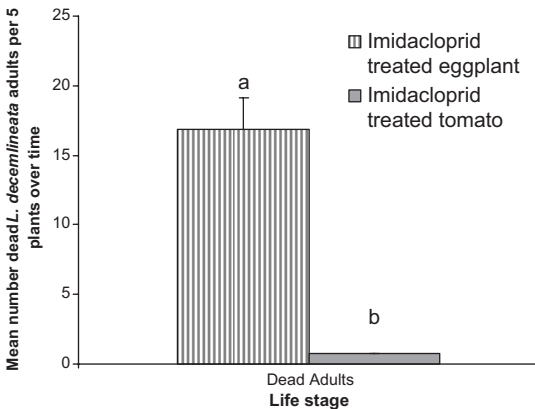


Fig. 2. Number of dead *L. decemlineata* adults (mean \pm SE per five plants) on imidacloprid-treated eggplant and tomato across seven sample dates in 2005. Bars surmounted by different letters are significantly different as determined by one-way ANOVA ($P < 0.05$) and Fisher protected LSD.

Table 2. Paired *t*-test results for live and dead *L. decemlineata* adults for all sample dates on untreated eggplant and potato and imidacloprid-treated eggplant and potato, 2006 and 2007

Sample date	Experiment 1 Live Adults (Untreated eggplant and potato)			Experiment 2 Dead Adults (Imidacloprid-treated eggplant and potato)		
	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>
16 May 2006	5.09	3	0.0147*	1.23	3	0.3071
19 May 2006	1.93	3	0.1487	0.54	3	0.6264
22 May 2006	2.76	3	0.0703	1.59	3	0.2109
26 May 2006	0.21	3	0.8454	1.12	3	0.3455
15 June 2007a	1.96	3	0.1449	1.33	3	0.2579
15 June 2007b	0.49	3	0.6578	0.11	3	0.9196
19 June 2007a	1.06	3	0.3660	0.21	3	0.8480
19 June 2007b	0.58	3	0.6013	0.72	3	0.5223
22 June 2007a	1.71	3	0.1862	0.96	3	0.4058
22 June 2007b	1.88	3	0.1566	0.13	3	0.9023
26 June 2007a	0.32	3	0.7704	0.33	3	0.7654
26 June 2007b	1.96	3	0.1449	0.43	3	0.6971

* Statistically significant at $\alpha = 0.05$ as determined by *t*-test.

1926, Visser and Piron 1998). Using such experiments, researchers have demonstrated that adult *L. decemlineata* are attracted to volatiles produced from potato plants (McIndoo 1926, Schanz, 1953, De Wilde et al. 1969, Visser 1976), and in particular, plants that have been fed upon by beetles or artificially damaged (Bolter et al. 1997, Schütz et al. 1997, Landolt et al. 1999). A three-component kairomone is comprised of (Z)-3-hexenyl acetate, (\pm)-linalool, and methyl salicylate, and it is attractive to both larvae and adult *L. decemlineata* (Dickens 2000, 2002).

In our olfactometer choice tests, using mechanically damaged foliage, field-collected *L. decemlineata* chose potato volatiles over eggplant or tomato, and chose eggplant over tomato. In similar choice tests, Dickens (2000) found that although *L. decemlineata* chose potato volatiles over soybean, there was no preference when offered potato versus tomato foliage. Among several possibilities, the difference in preference between potato and tomato foliage observed in our current study and the previous study (Dickens 2000) could be due to differences in cultivars of potato (*S. tuberosum* Superior in our current study versus *S. tuberosum* 'Kennebec' in Dickens 2000) and tomato (*L. esculentum* Florida 47 in our current study versus *L. esculentum* variety 'Pik Red' in Dickens 2000) used in the two studies.

Moreover, the difference in the response to potato over tomato between our study and that of Dickens (2000) demonstrates that there can even be variability (geographic or physiological) in the response of *L. decemlineata* to plant volatiles. This goes beyond the well-documented variability in *L. decemlineata* to colonize and feed more on one plant species or another in the field (Hsiao 1978, De Wilde and Hsiao 1981, Hare and Kennedy 1986). Moreover, such variations may be due to ecological differences such as availability of acceptable food sources (Fox and Morrow 1981, Thompson 1988, Bowers et al. 1992, Funk and Bernays 2001). In some cases, preferences may change on a seasonal basis (Rauscher 1980).

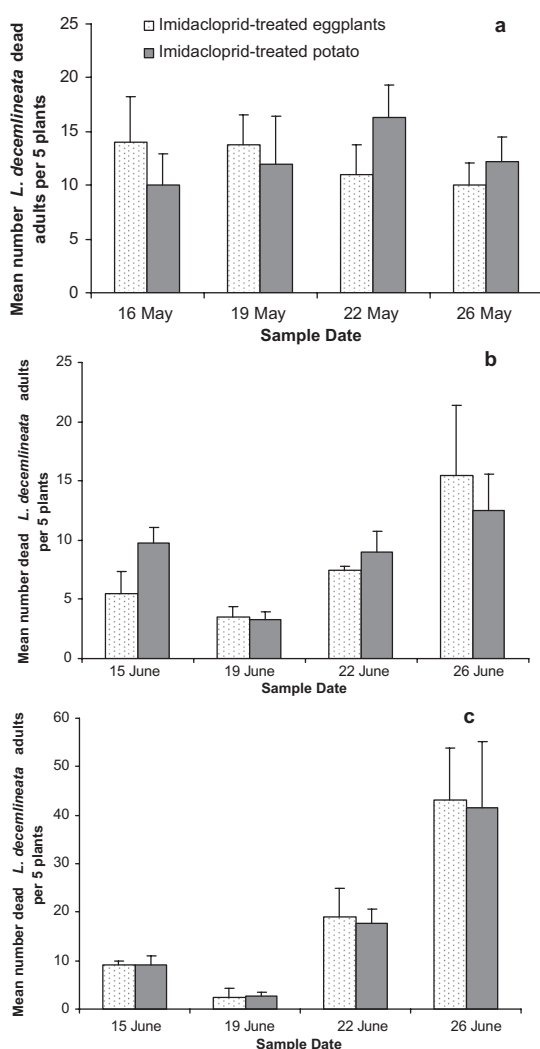


Fig. 4. Number of dead *L. decemlineata* adults (mean \pm SE per five plants) on imidacloprid treated eggplant and paired plots for four sample dates in 2006 (a), 2007a (b), and 2007b (c).

Host plant choice experiments conducted in the field can reveal useful information as well. Although it is virtually impossible to determine precisely what factors are playing a role in host plant choice in field experiments, it is nonetheless, essential to observe the behavior of the insect under natural conditions. The presence of live insects on a plant in the field is governed not only by the ability of the insect to find the plant but also by the acceptability of the plant to the insect for feeding, reproduction, or both. However, counts of dead adult insects on or around insecticide-treated plants can reveal more targeted information on the initial attraction to plants.

In our field host plant choice experiments, significantly more live *L. decemlineata* occurred on untreated eggplant than tomato or pepper and more dead *L. decemlineata* occurred on imidacloprid-

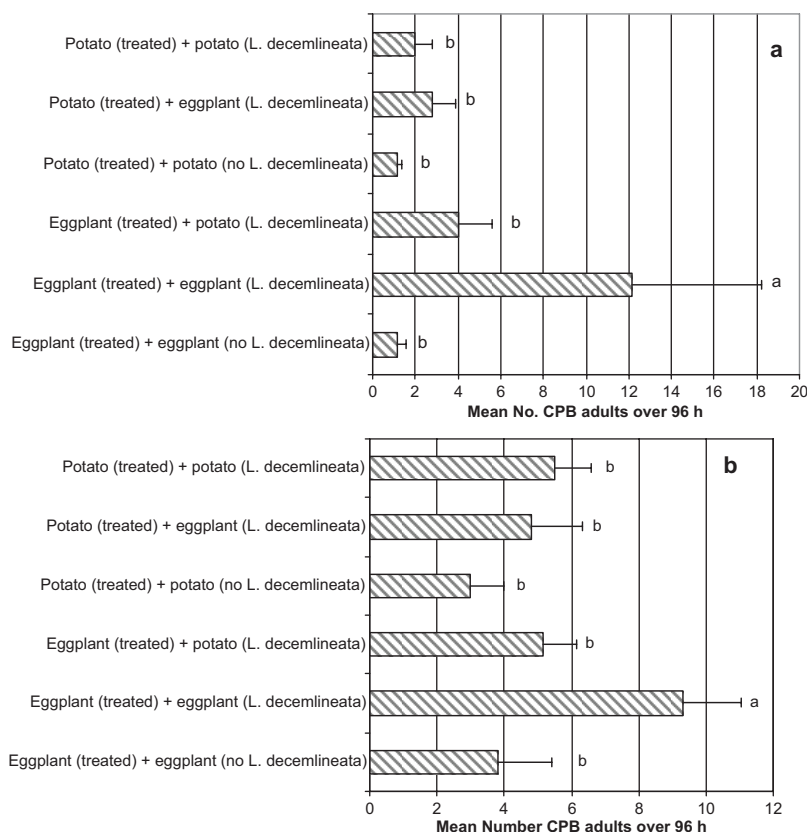


Fig. 5. Mean \pm SE cumulative numbers of *L. decemlineata* adults coming to combinations of paired eggplant and potato plants (*L. decemlineata*, two males per plant) over 96 h in 2006 (a) and 2007 (b). Bars surmounted by different letters are significantly different as determined by ANOVA ($P < 0.05$) and Fisher protected LSD.

treated eggplant than tomato or pepper. Thus, there was a field preference for eggplant that probably occurred at the initial plant colonization stage. Similar studies conducted with untreated and insecticide-treated eggplant and potato showed no preference for either species in the field. However, when adult male *L. decemlineata* were caged on eggplant versus potato plants in the field, there was significant attraction to eggplant. These results suggest that the presence of conspecific adult males can impact orientation of adults to susceptible host plants and potentially influence host plant selection in *L. decemlineata*.

One explanation for this phenomenon can be attributed to a male-produced aggregation pheromone of *L. decemlineata*, which was recently identified by Dickens et al. (2002). The pheromone is composed of a single enantiomer, (S)-3,7-dimethyl-2-oxo-oct-6-ene-1,3-diol, and it is attractive to both male and female beetles in the laboratory and in the field (Dickens et al. 2002, Kuhar et al. 2006a). It is possible that beetles feeding on eggplant produce more of the pheromone than beetles feeding on potato. Moreover, the combination of host plant volatiles and an aggregation pheromone can evoke a greater response than the individual components alone (Dickens 1989, 2000, 2006). Although additional studies are necessary to

quantify the effect host plant has on pheromone production by *L. decemlineata* male beetles, it is evident that orientation to host plants is a complex phenomenon. These studies, however, have led to a better understanding of host plant selection in *L. decemlineata*, and they may contribute to the exploration of alternative strategies for management of *L. decemlineata* populations.

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References Cited

- Analytical Software. 1998. Statistix for Windows user's manual. Analytical Software, Tallahassee, FL.
- Bolter, C. J., M. Dicke, J. J. A. Van Loon, J. H. Visser, and M. A. Posthumus. 1997. Attraction of Colorado potato beetle to herbivore-damaged plants during herbivory and after its termination. *J. Chem. Ecol.* 23: 1003–1023.
- Bowers, M. D., N. E. Stamp, and S. K. Collinge. 1992. Early stage of host range expansions by a specialist herbivore, *Euphydryas phaeton* (Nymphalidae). *Ecology* 73: 526–536.

- Brues, C. T. 1940. Food preferences of the Colorado potato beetle, *Leptinotarsa decemlineata* Say. *Psyche* 47: 38–43.
- De Wilde, J., J. K. Hille Ris Lambers-Suverkropp, and A. Van Tol. 1969. Responses to air flow and airborne plant odour in the Colorado potato beetle. *Neth. J. Plant Pathol.* 75: 53–57.
- De Wilde, J., and T. H. Hsiao. 1981. Geographic diversity of the Colorado potato beetle and its infestation in Eurasia, pp. 47–68. *In* J. H. Lashomb and R. A. Casagrande [eds.], *Advances in potato pest management*. Hutchinson & Ross, Stroudsburg, PA.
- Dickens, J. C. 1989. Green leaf volatiles enhance aggregation pheromone of boll weevil, *Anthonomus grandis*. *Entomol. Exp. Appl.* 52: 191–203.
- Dickens, J. C. 1999. Predator-prey interactions: olfactory adaptations of generalist and specialist predators. *Agric. For. Entomol.* 1: 47–54.
- Dickens, J. C. 2000. Orientation of Colorado potato beetle to natural and synthetic blends of volatiles emitted by potato plants. *Agric. For. Entomol.* 2: 167–172.
- Dickens, J. C. 2002. Behavioral response of larvae of the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) to host plant volatile blends attractive to adults. *Agric. For. Entomol.* 4: 309–314.
- Dickens, J. D., J. E. Oliver, B. Hollister, J. C. Davis, and J. A. Klun. 2002. Breaking a paradigm: male-produced aggregation pheromone for the Colorado potato beetle. *J. Exp. Biol.* 205: 1925–1933.
- Dickens, J. C. 2006. Plant volatiles moderate response to aggregation pheromone in Colorado potato beetle. *J. Appl. Entomol.* 130: 26–31.
- Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? *Science* (Wash., D.C.) 211: 887–893.
- Funk, D. J., and E. A. Bernays. 2001. Geographic variation in host specificity reveals host range evolution in *Uroleucon ambrosiae* aphids. *Ecology* 82: 726–739.
- Hare, J. D. 1990. Ecology and management of the Colorado potato beetle. *Annu. Rev. Entomol.* 35: 81–100.
- Hare, J. D., and G. G. Kennedy. 1986. Genetic variations in plant-insect associations: survival of *Leptinotarsa decemlineata* populations on *Solanum carolinense*. *Evolution* 40: 1031–1043.
- Hsiao, T. H. 1978. Host plant adaptations among geographic populations of the Colorado potato beetle. *Entomol. Exp. Appl.* 24: 437–447.
- Hsiao, T. H., and G. Fraenkel. 1968. Selection and specificity of the Colorado potato beetle for solanaceous and nonsolanaceous plants. *Ann. Entomol. Soc. Am.* 61: 493–503.
- Hunt, D. W. A., and G. Whitfield. 1996. Potato trap crops for control of Colorado potato beetle (Coleoptera: Chrysomelidae) in tomatoes. *Can. Entomol.* 128: 407–412.
- Jacques, R. L. 1988. The potato beetles: the genus *Leptinotarsa* in North America (Coleoptera, Chrysomelidae). E. J. Brill, New York.
- Jacques, R. L. 2005. University of Florida Institute of Food and Agricultural Sciences Featured Creatures: Colorado potato beetle. (http://creatures.ifas.ufl.edu/veg/leaf/potato_beetles.htm).
- Kuhar, T. P., K. Mori, and J. C. Dickens. 2006a. Potential of a synthetic aggregation pheromone for integrated pest management of Colorado potato beetle. *Agric. For. Entomol.* 8: 77–81.
- Kuhar, T. P., S. B. Phillips, R. A. Straw, C. Waldenmaier, and H. P. Wilson. 2006b. Commercial vegetable production recommendations, pp. F132–F138. Virginia Cooperative Extension, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- Landolt, P. J., J. H. Tumlinson, and D. H. Alborn. 1999. Attraction of Colorado potato beetle (Coleoptera: Chrysomelidae) to damaged and chemically induced potato plants. *Environ. Entomol.* 28: 973–978.
- Matsuda, K. 1988. Feeding stimulants of leaf beetles, pp. 41–56. *In* P. Jolivet, E. Petitpierre, and T. H. Hsiao [eds.], *Biology of Chrysomelidae*. Kluwer Academic Publishers, Amsterdam, The Netherlands.
- McIndoo, N. E. 1926. An insect olfactometer. *J. Econ. Entomol.* 19: 545–571.
- Ott, R. L., and M. Longnecker. 2001. An introduction to statistical methods and data analysis, 5th ed. Duxbury, Pacific Grove, CA.
- Rauscher, M. D. 1980. Host abundance, juvenile survival, and oviposition preference in *Battus philenor*. *Evolution* 34: 342–355.
- Rivnay, E. 1928. External morphology of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). *J. N Y Entomol. Soc.* 36: 125–145.
- Schanz, M. 1953. Der geruchssinn des kartoffelkafers (*Leptinotarsa decemlineata*). *Z. Vergl. Physiol.* 35: 353–379.
- Schütz, S., B. Weissbecker, A. Klein, and H. E. Hummel. 1997. Host plant selection of the Colorado potato beetle as influenced by damage induced volatiles of the potato plant. *Naturwissenschaften* 84: 212–217.
- Thompson, J. N. 1988. Variation in preference and specificity in monophagous and oligophagous swallowtail butterflies. *Evolution* 42: 118–128.
- Visser, J. H. 1976. The design of a low-speed wind tunnel as an instrument for the study of olfactory orientation in the Colorado potato beetle (*Leptinotarsa decemlineata*). *Entomol. Exp. Appl.* 20: 275–288.
- Visser, J. H., and P. G. M. Piron. 1998. An open Y-track olfactometer for recording aphid behavioural responses to plant odours, pp. 41–46. *In* *Proceedings of the Section of Experimental and Applied Entomology of The Netherlands Entomological Society*, Amsterdam, The Netherlands.
- Walsh, B. D. 1865. The new potato-bug and its natural history. *Pract. Entomol.* 1: 1–4.
- Zehnder, G., and J. Speese, III. 1987. Assessment of color response and flight activity of *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) using window flight traps. *Environ. Entomol.* 16: 1199–1202.

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